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Remarks on the fossil record and suprageneric nomenclature of barbets (Aves: Ramphastidae)

by Storrs L. Olson

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Prum (1988), in expanding on Burton's (1984) observation that the divergence of toucans occurred *within* the family of barbets (Capitonidae), provided a convincing case for including these groups in the same family-level taxon, the name Ramphastidae having priority. In their osteological studies of the Pici, both Prum (1988) and Simpson & Cracraft (1981) emphasized cranial characters at the expense of postcranial ones, which might still be investigated profitably. For example, toucans and barbets share a highly distinctive, presumably derived, morphology of the coracoid that is not found in other members of the Pici. Here, however, I would call attention to errors of interpretation by Prum (1988) in the fossil record and biogeography of barbets, and to errors in nomenclature of subfamilies and tribes that he either introduced or perpetuated.

The taxonomic status of the fossil genus *Capitonides*

Ballmann (1969a) described a new genus and species of barbet, *Capitonides europaeus*, from a carpometacarpus from a mid-Miocene fissure-fill in Bavaria. He referred a tarsometatarsus and humerus from the same site to "*Capitonides* sp.". A carpometacarpus from the Miocene at Grive-Saint-Alban, France, was assigned only to the Capitonidae and was considered to belong to a species more similar to living barbets than was *Capitonides* (Ballmann (1969b).

In the original description, Ballmann (1969a) stated that he had no skeletons of the modern genus *Trachyphonus* for comparison but he considered it unlikely that *Capitonides* would prove to be like any living genus. Later, Ballmann (1983) described *Capitonides protractus* from a humerus, ulna, carpometacarpus and tarsometatarsus from the middle Miocene Nördlinger Ries of southern Germany. At this time he realized that *C. protractus* was actually quite closely related to the living African genus *Trachyphonus*, which he found to be osteologically primitive and quite distinct from other barbets, a fact that may have influenced his original assessment that *Capitonides* would not prove to be similar to living genera.

Once he discovered their similarity to one another, however, Ballmann (1983) did not discuss such characters as might separate *Capitonides* from *Trachyphonus*, except to note that the former supposedly had a "relatively shorter" carpometacarpus. Whereas the proportions in *Capitonides* seem rather different from those of other genera of barbets (Ballmann 1983, Table 1), *Capitonides* (carpometacarpus 46.2% of humerus length) shows negligible difference from *Trachyphonus* (47.2–49.2%). In comparing Ballmann's illustrations with modern specimens, I see nothing that will distinguish these fossils from *Trachyphonus*.

Ballmann's (1983: 48) only biogeographical or paleoecological conclusion was that "a barbet indicates that the winters must have been mild enough to allow the growth of evergreen vegetation with fruits or berries during the whole year". This is an interesting but unexceptional conclusion that is consonant with other paleontological evidence and only requires that the fossils in question be of a barbet.

Prum (1988) criticised Ballmann's association of *Capitonides* with the Capitonidae and with *Trachyphonus* as being based partially on primitive characters. This confuses phylogeny reconstruction with the process of identification, which involves assessment of the sum of all characters, regardless of polarity. If *Trachyphonus* differs from other barbets by the retention of primitive characters, and the fossils possess these same characters and are otherwise not significantly different from *Trachyphonus*, what basis is there for identifying the fossils as anything other than barbets related to *Trachyphonus*?

Prum (1988) seized on a single character in one of Ballmann's (1983) line drawings, the supposed single instead of double canal in the hypotarsus of the tarsometatarsus of *Capitonides protractus*, as showing that this taxon was the sister-group of the entire suborder Pici. As a consequence, he erected a new family Capitonididae for the genus *Capitonides* (despite the fact that the type species, *C. europaeus*, is known only from a carpometacarpus and cannot be ascertained as having possessed the only character ascribed to the family). He further considered that no paleoecological inferences could be drawn from these fossils because they could not be shown to be barbets.

The erection of a new family based on a single such character is bad enough, but to do so without verifying that Ballmann's drawing was accurate or that this character was not attributable to breakage in the fossil is certainly not the best procedure. Nor was any consideration given to the possible ontogenetic or phylogenetic development of this character, or the amount of variation among individuals.

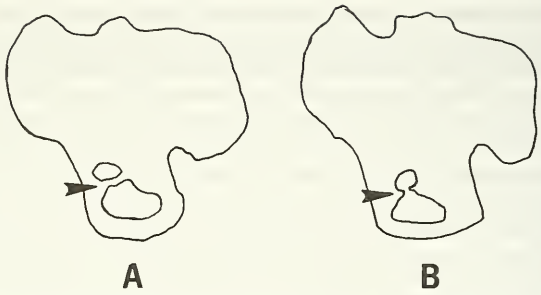

Figure 1. Proximal view of right tarsometatarsi in two species of toucans (Ramphastinae) to show individual variation in ossification of the small septum (arrows) dividing the hypotarsal loop enclosing the flexor tendons: A, *Andigena nigrirostris* USNM 428774; B, *A. hypoglauca* USNM 428789. The presence or absence of this septum determines whether there are one or two hypotarsal canals, but changes neither the number nor placement of the flexor tendons.

We are not talking here about the development of some significant evolutionary novelty. The change from a single to a double hypotarsal canal does not involve the addition of a new canal or the displacement of flexor tendons, but nothing more than the ossification of a septum between two already discrete portions of the original single canal (Fig. 1). Perhaps all members of the Pici progress from the single to the double condition during their ontogeny by such ossification, which in turn may have taken place several times during the phylogeny of the Pici. Very little searching among modern skeletons was needed to find an example within the Pici (an individual of the toucan *Andigena hypoglauca*) in which this ossified septum was lacking, leaving it with a single hypotarsal canal (Fig. 1). This character probably has little or no phylogenetic significance. If it really is present in *Capitonides protractus*, which, after all, is more than 15 million years old, why should this not simply be regarded as a minor primitive condition? If so, it would certainly not provide a basis for the creation of a new family.

Capitonides protractus appears to be referable to the modern genus *Trachyphonus*, and the type species, *C. europaeus*, may be as well. I reject the name Capitonididae Prum, 1988, as a junior synonym of Ramphastidae Vigors, 1825, in the newly expanded sense, and as a junior synonym of Capitonidae Bonaparte, 1846, in the traditional sense. Because *Capitonides* and *Trachyphonus* surely belong to the same subfamilial group, if not the same genus, as first revisor I regard Trachyphoninae Prum, 1988, as taking precedence over Capitonididae Prum, 1988.

Suprageneric nomenclature

Prum's (1988) classification resulted in the recognition of 10 suprageneric taxa within the expanded family Ramphastidae, of which 7 were proposed as new. Three of these names, one of which does not have Prum's authorship, are grammatically incorrect. There already exist well-known avian

family-group names with the stems *bucco* (Bucconidae) and *ornis* (e.g. Threskiornithidae) to serve as models. The first use of Megalaiminae is traceable to Sundevall (1873: 75, where spelled Megalaeminae). Erroneous renderings in Prum (1988) and their corrections are listed below:

Erroneous	Grammatically correct
Gymnobuccini	**Gymnobucconini**
Megalaiminae	**Megalaimatinae**
Semnorninae	**Semnornithinae.**

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Sexual dimorphism in Meller's Duck *Anas melleri*

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First described in 1864, Meller's Duck *Anas melleri* has generally been considered to have similar sexes (Sclater 1864, Hubbard 1907, Phillips 1922, Delacour 1956, Johnsgard 1978), although Darby (1978) and Madge & Burn (1988) have suggested that males may be darker than females and Todd (1979) that males have brighter legs and feet. Like other members of the genus, both sexes have their own calls; see Johnsgard (1978).

Anas melleri is poorly known in Madagascar (where it is endemic) and very few specimens have been held in captivity. The species is also poorly represented in museums; thus there are only 13 skins, collected in